indeed he played the major role in its development. But the idea originated with Price, in an unpublished manuscript that Maynard Smith had reviewed for *Nature*. Maynard Smith later explained that "Dr Price is better at having ideas than at publishing them. The best I can do therefore is to acknowledge that if there is anything in the idea the credit should go to Dr Price and not to me".

Price's inability to focus on publishing his theoretical insights was due to a sudden religious experience in the summer of 1970 and a shift of priorities in his life. It is not known what in particular led Price, formerly a hardline atheist, down this avenue, although he did mention to Hamilton that a series of coincidences had forced him to conclude that God existed. He came to regard his equation as a gift from God and, taking a very literal interpretation of the New Testament, gave up science in order to dedicate his life to altruism. He sheltered the homeless in his flat, and gave away all his money and possessions to the poor and needy, and his life spiralled out of control. He became deeply depressed shortly after Christmas of 1974, and was found dead in his squatter's tenement on the 6th of January 1975. He had cut his throat with nail scissors.

Further reading

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Institute of Evolutionary Biology, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK.
E-mail: andy.gardner@ed.ac.uk

Correspondence

Meaningful call combinations in a non-human primate

Kate Arnold and Klaus Zuberbühler

Human speech is based on rule-governed assemblage of morphemes into more complex vocal expressions. Free-ranging putty-nosed monkeys (*Cercopithecus nictitans*) provide an interesting analogy, because males combine two loud alarm calls, 'hacks' and 'pyows', into different call series depending on external events [1]. Series consisting of 'pyows' are a common response to leopards, while 'hacks' or 'hacks' followed by 'pyows' are regularly given to crowned eagles [2,3]. Sometimes, males produce a further sequence, consisting of 1–4 'pyows' followed by 1–4 'hacks'. These 'pyow–hack' (P–H) sequences can occur alone, or they are inserted at or near the beginning of another call series. Regardless of context, P–H sequences reliably predict forthcoming group progression [4]. In playback experiments, we tested the monkeys' reactions to 'pyows', 'hacks' and P–H sequences and found that responses matched the natural conditions. Specifically, females started group progressions after hearing P–H sequences and responded appropriately to the other call series. In a second experiment, we tested artificially composed P–H sequences, and found that they were also effective in eliciting group progressions. In a third experiment, we established that group movement could only be triggered by the calls of the group's own male, not those of a stranger. We conclude that, in this primate, meaning is encoded by call sequences, not individual calls. Many birds and primates are limited by small vocal repertoires [5,6], and this constraint may have favored the evolution of such combinatorial signaling.

We designed playback experiments to investigate whether P–H sequences given by a male are causally responsible for eliciting

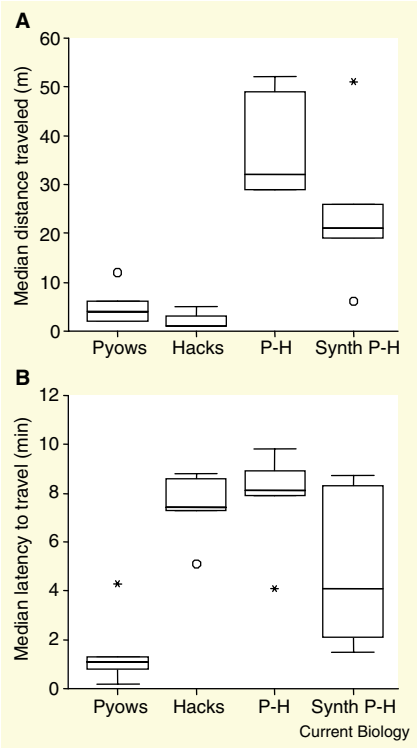

Figure 1. Median distance traveled (A) and median latency to travel (B) after hearing playbacks of different call series by the group's male: 'pyow' series, 'hack' series, natural P–H sequences (P–H), and artificially composed P–H sequences (Synth P–H).

Box plots indicate medians, inter-quartiles and ranges; outliers are indicated by open circles.

travel in individual group members. We conducted a series of playback experiments with free-ranging putty-nosed monkeys at Gashaka Gumti National Park, Nigeria. In a first experiment, we observed the behavior of the females of a habituated group in response to playbacks of natural call series of their own male. A female could serve as focal subject if she was located at the periphery of the group while the male was at the opposite side, hereby ensuring that the male's calls emanated from the correct direction. Playback trials consisted of five 'hacks', five 'pyows' or a five-call P–H sequence. Using a GPS unit, the focal female's location was marked prior to and 20 min after playback, while her behavior was monitored continuously.

Our results showed that playback of 'hack' series (usually indicating eagle presence) inhibited movement in females (median = 1.0 m) and

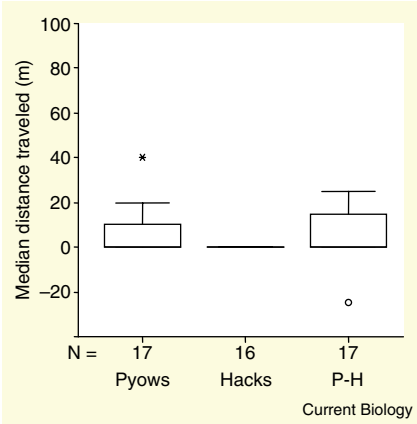

Figure 2. Median distance traveled towards the playback speaker by females after hearing playbacks of 'pyow' series, 'hack' series or P–H sequences by a stranger male.

Box plots indicate medians, inter-quartiles and ranges; outliers are indicated by open circles; extremes are indicated by stars.

caused long latencies to move (median = 7.4 min), as under natural conditions. Playback of 'pyows' (indicating a range of disturbances, including leopard presence) elicited relatively rapid responses (median = 1.1 min), although the distance traveled towards the speaker was small (median = 4.0 m). Movement was often accompanied by scanning behavior in the direction of the calls, as if trying to acquire additional information about the cause, a pattern also seen to natural 'pyows'. P–H sequences resulted in significant travel towards the calls (median = 32.0 m), although females only responded slowly (median = 8.1 min). Statistically, both travel distance and latencies differed significantly across the three conditions (Figure 1A: $n_H = n_P = n_{P-H} = 5$, d.f. = 2, $\chi^2 = 8.4$, p = 0.008; Figure 1B: $n_H = n_P = n_{P-H} = 5$, d.f. = 2, $\chi^2 = 7.6$, p = 0.024, Friedman tests, two-tailed; see Supplemental data for individual responses, post-hoc analyses, and comparisons with natural responses).

At this point, it could be argued that there were subtle acoustic differences between 'pyows' and 'hacks' produced as part of P–H sequences compared to calls given in response to predators, and that listeners responded to these differences, rather than call combinations. Although acoustic analyses did not support this hypothesis (see the Supplemental data available on-line with this issue) we carried out a second experiment, this time using artificially composed P–H sequences edited from 'pyows' and 'hacks' originally given to predator stimuli. We found no differences between artificial and natural P–H sequences in the distance traveled by females and their response latencies ($P–H_{real}$ median = 32.0 m, $P–H_{synthesised}$ median = 21.0 m: Wilcoxon signed ranks test, $n_1 = n_2 = 5$, z = –1.483, p = 0.188; $P–H_{real}$ median = 8.1 min, $P–H_{synthesised}$ median = 4.1 min: Wilcoxon signed ranks test, $n_1 = n_2 = 5$, z = –1.214, p = 0.313; Figure 1). We concluded that the communicatively salient property of the signal was how calls were assembled, rather than any context-specific acoustic variation within 'pyows' or 'hacks'.

In a final experiment, we investigated whether females discriminated between calls given by their own male compared to other males of the same population. At our study site, monkey groups are often surrounded by neighbors, suggesting that females should be selective in their responses when hearing male calls, particularly to P–H sequences. We repeated the first experiment, this time testing various unhabituated groups within a 32 km^2 study area. In response to 'pyows' and P–H sequences some females traveled towards the speaker (35.5%, 29.4% of trials, respectively) but never in response to 'hacks' (0.0%). However, approaches were only observed in a small number of females (median = 2.0) and only in association with their own male. All remaining group members stayed behind regardless of stimulus type, so that the median travel distances to all stimuli were negligible (median = 0.0 m in all conditions; Kruskal-Wallis, $n_1 = 16$, $n_2 = n_3 = 17$, d.f. = 2, $\chi^2 = 5.177$, p = 0.075; Figure 2), confirming that females discriminated between call sequences by their own and those of stranger males, especially in response to P–H sequences.

Our study has demonstrated that putty-nosed monkey call combinations convey at least three types of information: the event witnessed by the male, the caller's identity, and whether he intends to travel, all of which are recognized by other monkeys. We conclude that, contrary to current theory, meaningful combinatorial signals have evolved in primate communication [7–9] and future work may reveal further examples. Many forest primates and most bird species are limited by small vocal repertoires [5,10], and this constraint may have favored the evolution of combinatorial signals. The exact psychological mechanism of how the observed semantic changes are achieved when two call types interact in a sequence, however, is a matter for further investigation.

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Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/5/R202/DC1

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School of Psychology, University of St Andrews, St Andrews, KY16 9JP, Scotland, UK.
E-mail: kz3@st-andrews.ac.uk